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Effects of Fire on Soil CO_2 Efflux in a Mature Longleaf Pine Forest

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EFFECTS OF FIRE ON SOIL CO_2 EFFLUX IN A MATURE

LONGLEAF PINE FOREST

by

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for the Degree of Master of Science

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ABSTRACT

EFFECTS OF FIRE ON SOIL CO_2 EFFLUX IN A MATURE

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This study was conducted from 2012-2013 in a 96 year old longleaf pine at the Lake Thoreau Environmental Center located Lamar County, MS. Measurements of soil CO_2 efflux (i.e., soil respiration or SR) rates (µmol m^{-2} sec^{-1}) were taken across 8 field plots (4 burned, 4 unburned) before and after a prescribed fire on that occurred in May, 2012. These measurements were taken over diurnal cycles using a LICOR LI-8100A automated soil gas flux system with long term chambers. SR rates and soil temperature measurements were collected during 3 sampling periods in 2012 and 1 sampling period in 2013, which were split into seasonal sampling periods: a pre-burn, spring 2012 period (April & May), a post-burn, summer 2012 period (June, July, & August), a post-burn, fall 2012 period (November), and a post-burn, spring 2013 period (April & May). Overall, the unburned plots had significantly greater mean SR than the burned plots (2.57 vs. 3.57 µmol m^{-2} sec^{-1}, p=0.04). After combining SR and soil temperature across seasons, soil temperature explained 59% of the variability in SR on the burned treatment (p <0.0001) and 71% of the variability in SR on the unburned treatment (p <0.0001).

ACKNOWLEDGMENTS

This monumental undertaking would have not been possible without the guidance and patience of major professor Dr. Micheal A. Davis., and graduate committee Dr. Kevin A. Kuehn and Dr. Carl P. Qualls. Also, the USM Department of Biological Sciences Department staff was integral in carrying out this project. Special thanks to the people that helped with the immense amount of field work associated with this project: Ethan Currie, Jerrid Boyette, Stephanie Koury, Jay Price, and Brandy Purdy.

DEDICATION

I would like to dedicate this work in loving memory of my parents Richard H. Flowers, Jr. & Brenda B. Flowers. Without their guidance in life I would never be the person that I am today. They planted a seed of interest in biology at an early age that has bloomed into the love of the field that I carry with me in my life.

"The day you become an adult is the day the path you follow becomes the path that you lead." KLF

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LIST OF ABBREVIATIONS

LLP	Longleaf Pine Preserve
USM	The University of Southern Mississippi
IRGA	Infrared Gas Analyzer
MFC	Mississippi Forestry Commission
SOC	Soil Organic Carbon
SD	Standard Deviation
SE	Standard Error
SR	Soil CO_2 Efflux
ST	Soil Temperature

CHAPTER I - INTRODUCTION

Protecting viable habitats and restoring habitats in decline is paramount to preserving ecological resources and the ecosystem services those habitats provide. The southeastern United States is home to the longleaf pine (*Pinus palustris*) savanna ecosystem that once spanned the majority of the southeastern Coastal Plain, from Texas to Virginia (Frost 1993). The longleaf pine savanna is a type of forest savanna ecosystem that provides habitat to many threatened or endangered plant and animal species that benefit from habitat maintained by frequent fire (Van Lear et al. 2005, Kirkman et al. 2010). Due to anthropogenic expansion, extensive timber harvesting, and fire suppression, less than 3% of the historical extent of the longleaf pine ecosystem in the southeastern United States remains (Frost 1993).

The understories on longleaf pine forests are extremely diverse and provide habitat and forage for many wildlife species (Means 2006). The understory structure of these forests is primarily maintained by fire (Glitzenstein et al. 2003). Historically, these fires were ignited naturally by frequent lightning activity or by Native Americans (Fowler & Konopik 2007). Prescribed fire is the primary tool used for the management of longleaf pine understories today. Prescribed burning decreases the density of midstory plant species and allows for a more diverse understory and better regeneration of longleaf pine (Gilliam & Platt 1999). Frequent fire intervals, optimally around two years apart (Peterson & Reich 2008), are shown to increase plant species richness by providing a more heterogeneous habitat with varying fire intensity (Platt et al. 2006, Hiers et al. 2009, Ellair & Platt 2013). In the absence of fire, fuel loading increases, ultimately leading to greater fire intensity and potential ecosystem damage (Thaxton & Platt 2006).

Forest fires, particularly wildfires, can greatly alter carbon sequestration functions with increasing fire intensity due to increased fuel loading. Forest ecosystems serve as a major carbon pool in terrestrial ecosystems (Dixon et al. 1994, Goodale et al. 2002). Carbon cycling in longleaf pine and other forested ecosystems has been extensively studied in relation to carbon sequestration and carbon dioxide (CO_2) efflux (Vargas et al. 2010, Melillo et al. 2011, Samuelson & Whitaker 2012, Dilustro et al. 2005). Carbon cycling is an essential ecosystem service provided by forests in terrestrial ecosystems (Schlesinger & Andrews 2000, Goodale et al. 2002). It is equally important to understand how fire management practices affect these ecosystem services, given that fire is vital to maintaining a longleaf pine savanna ecosystem.

Soil CO_2 efflux (SR) is a measurement of the rate of CO_2 (μmol m^{-2} sec^{-1}) released from the soil over a given period of time. Within forest ecosystems, SR is primarily attributed to the heterotrophic respiration of micro-organisms (Zogg 1997), as well as autotrophic root respiration in the litter layer and organic layer of the soil (Guo et al. 2008). Climatic warming has been shown to increase metabolic activity in mesocosm studies (Yvon-Durocher et al. 2010), increasing overall ecosystem respiration by offsetting the balance of carbon being fixed through photosynthesis and released through CO_2 respiration. Understanding the effects of soil warming on increasing SR rates (Fang & Moncrieff 2001) and increasing organic matter decomposition rates in the litter layer (Sulzman et al. 2005, Groenigen et al. 2014) is essential to understanding the carbon flow in forest ecosystems. Quantifying SR rates can lead to identifying carbon sources and sinks, leading to better ecosystem management decisions from an ecosystem services perspective.

The moisture retention capabilities of the upper organic and duff layer of forest soil can affect the impacts of fire in relation to tree mortality and regrowth (Varner et al. 2007). Soil moisture has been shown to be a key component in mediating metabolic activity; in general increased metabolic activity is associated with increased soil moisture (Skopp et al. 1990). The macro- and micro-organism populations as well as plant roots in the upper layers of the soil and leaf litter have been shown to be negatively affected by fire, essentially sterilizing the soil and requiring recolonization for soil metabolic processes (SR) to resume (O'Brien et al. 2010). Leaf litter decomposition is also correlated to soil moisture. A study by Dilly and Munch (1996) in a black alder forest in Northern Germany showed a 50% increase in litter decomposition rates over a two year period on a site that maintained more soil moisture.

Soil nutrient cycling, primarily nitrogen (N) and phosphorus (P), is also affected by the frequency and occurrence of fire in forest ecosystems. Infrequent fire can result in the accumulation of coarse woody debris. This type of debris can comprise up to 24% of certain forest understories and can bind large amounts of N and P (Laiho & Prescott 1999). Fires associated with slash-and-burn clearing in tropical forests can transform N and P into forms more readily taken up by plants (Giardina et al. 2000). The majority of nitrogen is either lost through volatilization or transforms from organic to inorganic forms that are more readily available to be taken up by plants and microorganisms. Studies on P availability have indicated levels of orthophosphate, a more plant available form of P, to increase following a prescribed fire (Cade-Menum et al. 2000, Certini 2005). The increase available P following a prescribed fire can increase the plant and microbial productivity within the ecosystem.

The main purpose of this experiment was to quantify the effects of a prescribed burn on bulk SR rates from burned and unburned plots of longleaf pine savanna, across seasonal sampling periods. Soil temperature (°C) and leaf litter weight (g) data were also collected to help explain SR responses. The primary hypothesis was that mean SR rates on the burned treatments would be statistically the same as mean SR rates on the unburned treatments. Our secondary hypothesis was that mean SR rates would have a positive relationship with mean mass of the litter and mean soil temperature.

CHAPTER II – MATERIALS AND METHODS

Study Site

This experiment was conducted in 2012 and 2013 across the Longleaf Pine Preserve (LLP), a 160 acre preserve nested within the Lake Thoreau Environmental Center at the University of Southern Mississippi (USM). In 1897, the LLP property was signed over by President William McKinley from federal to private ownership. This property changed ownership several times and in 1916 it was donated to Mississippi Normal College (now USM) by the J.J. Newman Lumber Company. The forest was allowed to naturally regenerate and was thinned periodically primarily to remove undesirable loblolly pines (*Pinus taeda*) from the upland sites. The Mississippi Forestry Commission (MFC) periodically managed the site up until the late 1980s. Since then no management activities had been conducted and the forest went unburned for > 20 years (personal communication, Mike Lee, MFC District Forester, Southeast Division). In 2008, the Department of Biological Sciences at USM assumed management responsibilities of the LLP and in 2009 dormant season prescribed fire was conducted in order to reduce fuel loads. In 2010, the LLP was placed on a two-year prescribed fire rotation schedule with fires alternating between growing season and dormant season. Thus, the LLP was burned during the dormant season in 2010 (March) and the fire for this study was conducted during the growing season (May) in 2012.

The LLP has 296 permanent sampling points set on a 50m x 50m grid across the entire preserve. The LLP is also separated into burned and unburned zones for long-term studies that examine the management and restoration of mature longleaf pine forests (Fig. 1). For this study, twelve of these sampling points were randomly chosen within upland habitats with similar soils, primarily Freestone-McLaurin-Susquehanna association (Appendix A). Six of these points were in burned zones and six were in unburned zones (Table 1).

Table 1

Longleaf Preserve Research Plot Locations

Plot	Treatment	Stake Number(s) on Sampling Grid Plot Center Coordinates (°N, °W)
1	Burned (Center)	244,245,253,254 N31° 20.482' W89° 24.907'
2	Unburned (Center)	201,202,226,227 N31° 20.565' W89° 24.893'
3	Unburned (Center)	101, 102,103,126,127,128 N31° 20.679' W89° 24.883'
4	Burned (Center)	97,98,122,123 N31° 20.695' W89° 24.235'
5	Unburned (Center)	94,95,119,120 N31° 20.701' W89° 24.342'
6	Burned (Center)	116,117,141,142 N31° 20.672' W89° 24.432'
7	Unburned (Stake)	28 N31° 20.769' W89° 24.862'
8	Unburned (Stake)	53 N31° 20.739' W89° 24.863'
9	Unburned (Stake)	79 N31° 20.716' W89° 24.834'

Table 1 (continued).

10	Burned (Stake)	60 N31° 20.740' W89° 24.638'
11	Burned (Stake)	58 N31° 20.739' W89° 24.703'
12	Burned (Stake)	108 N31° 20.682' W89° 24.701'

Research plot number with corresponding fire treatment group, parentheses next to treatment designates the location of plot center either centered between stakes in the sampling grid or an independent sampling stake within the LLP sampling grid (Figure 1).

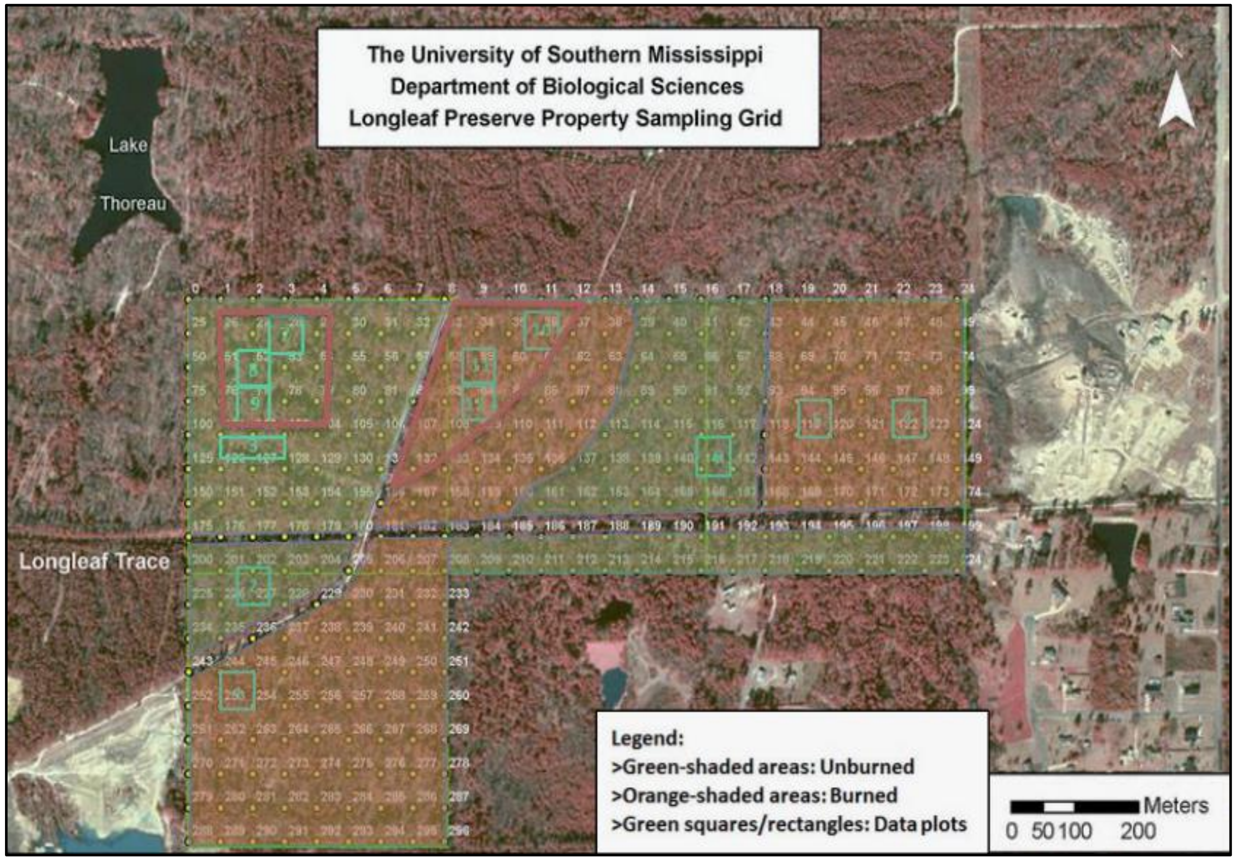


Figure 1. LLP Prescribed Burn Zones

The LLP sampling grid, located west of Hattiesburg. Green-shaded areas show unburned areas, orange-shaded areas show burned areas, and the green squares show the research plots (Produced by Michael Davis, PhD., used with permission).

Field Protocol

Soil Respiration Measurements

SR data were collected during the spring, summer, and fall seasons of 2012 and in the spring of 2013. Data were collected at each of the twelve points using a LI-8100 Infrared Gas Analyzer (IRGA) (LiCOR Inc., Lincoln, NB) and LI-8150 multiplexer with 4 long term automated chambers (LI-8100-104) that collected readings over a minimum period of 24 hours. This minimum period of time was established to encompass the variability of flux readings across plots due to changing environmental conditions and diurnal plant responses. At each of the twelve sampling points, four automated long term chambers were positioned atop polyvinyl chloride soil collars (soil area = 317.8 cm^2) inserted approximately 1-3 cm into the soil. The sampling quadrats at each point were randomly chosen within 4 azimuthal quadrants (NE, SE, SW, and NW) within 15 meters from the center of the plot (Table 2).

The chambers were left on the collars for 30 minutes before gathering readings to prevent an increase in CO_2 efflux due to the collar insertion (Maier & Kress 2000, Samuelson &Whitaker 2012). Readings were collected with each chamber for 3 minutes 30 seconds to reduce any gas build up within the chambers (Welles et al. 2001) and readings were repeated every 30 minutes over a 24-48 hour sampling period.

SR rates (µmol m^{-2} sec^{-1}) were calculated with the following equation:

Soil Efflux Calculation:

$$F_c = \frac{10VP_0(1-\frac{W_0}{1000})}{RS(T_0+273.15)}\frac{\partial C'}{\partial t} \qquad \text{Eq. (1)}$$

In the equation, F_c is the soil CO_2 efflux rate (μmol m^{-2} sec^{-1}), V is volume (cm^3), P_0 is the initial pressure (kPa), W_0 is the initial water vapor mole fraction (mmol/mol), R is the Universal Gas Constant, S is the soil surface area (cm^2), T is initial air temperature (°C), and $\frac{\partial C'}{\partial t}$ is the initial rate of change in water-corrected CO_2 mole fraction (μmol/mol) (from LICOR 8100 Manual, 2015).

Table 2

Location of Respiration Sampling Points within Research Plots

Plot	Sampling Point / Quadrant	Azimuth (degrees)
1	1 / NW	60
1	2 / NE	97
1	3 / SE	194
1	4 / SW	356
2	1 / NW	82
2	2 / NE	143
2	3 / SE	219
2	4 / SW	360
3	1 / NW	29
3	2 / NE	98
3	3 / SE	213
3	4 / SW	330
4	1 / NW	89
4	2 / NE	133
4	3 / SE	268
4	4 / SW	354
5	1 / NW	52
5	2 / NE	118
5	3 / SE	256
5	4 / SW	298
6	1 / NW	7
6	2 / NE	97
6	3 / SE	231
6	4 / SW	338

Table 2 (continued)

7	1 / NW	1
7	2 / NE	101
7	3 / SE	254
7	4 / SW	271
8	1 / NW	22
8	2 / NE	158
8	3 / SE	253
8	4 / SW	305
9	1 / NW	55
9	2 / NE	160
9	3 / SE	244
9	4 / SW	300
10	1 / NW	73
10	2 / NE	172
10	3 / SE	210
10	4 / SW	317
11	1 / NW	30
11	2 / NE	102
11	3 / SE	245
11	4 / SW	318
12	1 / NW	56
12	2 / NE	142
12	3 / SE	257
12	4 / SW	281

This table indicates the locations of the individual respiration reading within all treatment plots, 15 meters from the plot center on the azimuth indicated above. The plots were split into 4 sampling areas, split into 4 quadrants (NW, NE, SE, and SW).

Burned and unburned plots were paired by proximity and samples were taken from each point simultaneously using separate LI-8100 units so that variability in SR readings due to environmental conditions would be limited. Occasionally an LI-8100 unit malfunctioned and when this happened, the paired plots were sampled consecutively. The readings were grouped into pre-burn readings in the spring of 2012 (April & May), post-burn I readings in the summer of 2012 (June, July, & August), post-burn II readings in the fall of 2012 (November), and post-burn III readings in spring 2013 (March & April) (Figure 2).

Soil Temperature Measurements

Soil temperature (°C) data were collected simultaneously with SR data using a soil temperature thermistor connected to the LI-8100. These probes were inserted 5 cm into the soil within 30 cm of the soil collar to ensure accurate temperature readings were paired with each SR measurement.

Leaf Litter Measurements

Litter samples were taken from inside the SR soil collars prior to the pre-burn SR sampling in April 2012. A sharp knife was used to cut litter along the inside edge of the soil collars. Litter was collected down to bare mineral soil. Samples were placed into paper bags, oven-dried at 105 °C, and weighed (g) (Table 3). There were four samples per plot, with one sample per SR sampling point in each quadrant (NE, NW, SW, & SE).

A)

B)

C)

Figure 2. Post-burn 2012 Vegetation Re-emergence

Photographic representation of the effects of a prescribed burn on re-emergence of vegetation in plot 5 (2012) [A) 2 weeks post-burn, B) 6 months post-burn,, C) One year post burn].

Statistical Analyses

The SR (μmol m^{-2} sec^{-1}) and soil temperature (°C) measurements were proofed before analysis to ensure there were no false readings that would skew the statistical analyses. All SR measurements that ranged between 0-0.5 and > 9.5 μmol m^{-2} sec^{-1} were removed from analyses to decrease the likelihood of including a false reading. The readings that were wildly different from the previous and subsequent readings were removed from the analyses. SR measurements that consisted of a sample size less than 15 measurements due to equipment malfunctions were removed. An equipment malfunction necessitated that plots 1-4 be excluded from the statistical analyses because they were unable to be sampled during the post-burn summer 2012 and the post-burn spring 2013 periods. Plot 9 had a large number of false readings during the post-burn summer 2012 period and these were removed from the analyses, however, plot 9 remained in the data analyses for the other sampling periods.

Data were tested for the assumptions of normality and equal variances to determine whether parametric or non-parametric statistical hypothesis tests should be employed. The Shapiro-Wilk's goodness of fit test was used to check for normality within the groups across season and the Bartlett's test for unequal variance was used for determining if there was equal variance between the treatments. SR readings showed slight deviations from normality, but this is not unusual with such a large sample size and the sensitivity of these tests to larger sample sizes (Zar 2010). Some variability was accounted for by averaging the mean SR and temperature readings during the measurement periods. The statistical power in these tests was decreased by the variance between the groups, although that effect was decreased due to such a large data set.

Parametric tests were used in the analyses of this experiment. The pre-burn, spring 2012 mean SR, litter weight, and soil temperature data were analyzed by treatment with T-test analyses, comparing the mean measurements between the burned and unburned plots. The mean SR and soil temperature data from the post-burn I, II, & III sampling periods were also analyzed with T-tests, comparing the differences in measured means between the burned and unburned plots. The soil temperature data for the pre-burn, spring 2012 as well as post-burn I, II, and II sampling periods were analyzed for any significant effects on SR with linear regressions. A two factor ANOVA was used to analyze overall SR measurements by burn treatment and season. Appendix B contains daily mean SR and soil temperature readings grouped by treatment, season, and date with samples sizes (n) for both treatments used for the data analyses. Statistical analyses were conducted with JMP 12 (SAS Institute Inc., Cary, NC). All statistical analyses were interpreted for significance using an α of 0.05.

CHAPTER III - RESULTS

Pre-burn Spring 2012 Sampling Period

Plots in the unburned areas had significantly greater leaf litter biomass than those in the burned plots (*p*=0.0014) (Figure 3, Table 3). Unburned plots had leaf litter dry mass (n=16, mean=31.27 g, and ± SE=2.81) that was 69.1% greater than that of the burned plots (n=16, mean=52.89 g, and ± SE=5.24) (Figure 3).

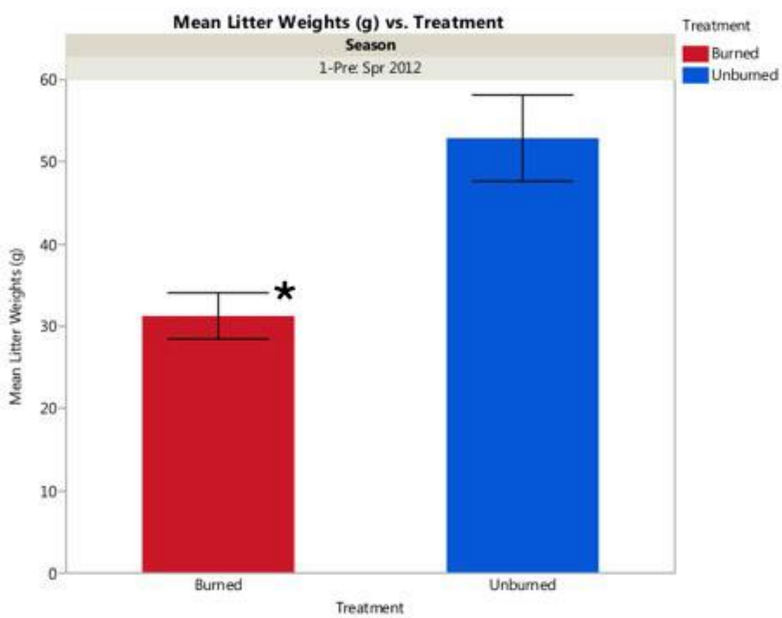


Figure 3. Mean Litter Weights by Treatment for Spring 2012

Mean leaf litter dry weights (g) from 2012 pre-burn sampling period with ± SE (Burned: n=16, Unburned: n=16).

Mean SR measurements (µmol m^{-2} sec^{-1}) for both treatments were calculated by compiling each 24 hour sampling period into one daily mean SR measurement. Mean SR rates for the burned (n=13, mean=3.39 µmol m^{-2} sec^{-1}, and ± SE=0.08) and unburned plots (n=18, mean=3.53 µmol m^{-2} sec^{-1}, and ± SE=0.18) were not significantly different during this sampling period (*p*=0.48) (Figure 4, Table 3).

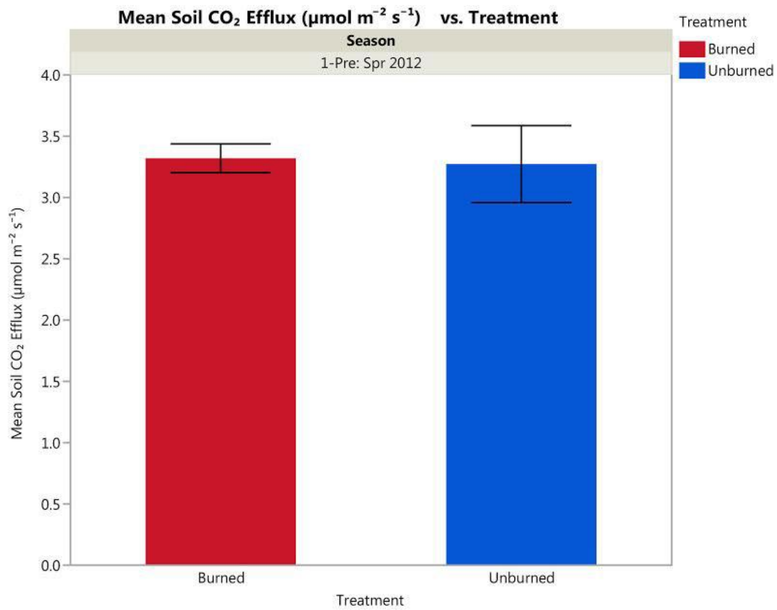


Figure 4. Mean SR by Treatment for Spring 2012

Mean soil CO_2 efflux (µmol m^{-2} sec^{-1}) from 2012 pre-burn sampling period with ± SE. (Burned: n=13, Unburned: n=18).

Mean soil temperature (°C) was also not significantly different for the burned (n=13, mean=20.4 °C, and ± SE=0.18) and unburned (n=18, mean=20.5 °C, and ± SE=0.46) treatments during the pre-burn spring 2012 sampling period (p=0.86) (Figure 5, Table 3).

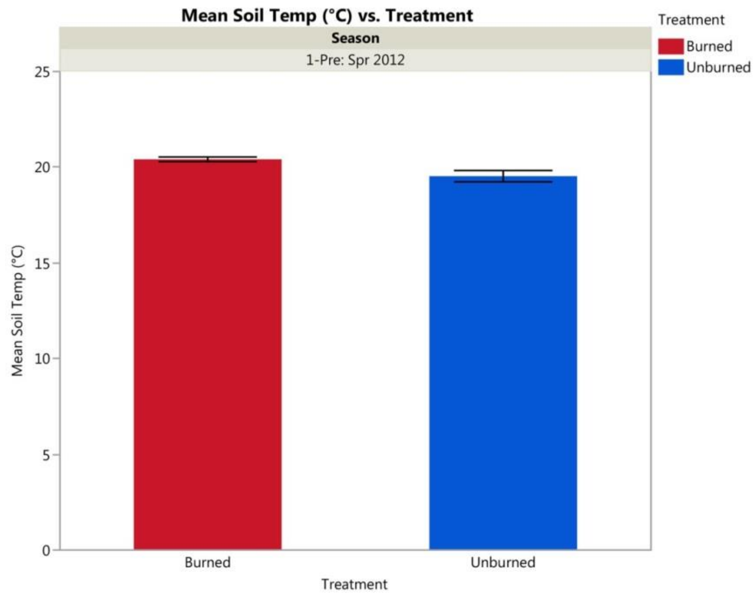


Figure 5. Mean ST by Treatment for Spring 2012

Mean soil temperature (°C) from 2012 pre-burn sampling period with ± SE (Burned: n=13, Unburned: n=18).

Multiple linear regressions were used to determine the relationship between measured SR (μmol m^{-2} sec^{-1}) in relation to litter weight (g) and soil temperature (°C) as well as litter weight versus soil temperature in the pre-burn spring 2012 sampling period (Figure 7, Table 4). The only significant correlation (p=0.04) that arose from the analyses on mean SR and mean litter weight was from the burned treatment ($F_{(1,13)}$=5.17). These results indicated that SR was negatively correlated with litter weight, which explained 29% of the variability seen in SR (Figure 7a). The linear regression between SR and soil temperature for the unburned treatment spring 2012 ($F_{(1,12)}$=6.52, p=0.02, R^2=0.32) sampling period indicated a significant positive correlation between soil temperature as a predictor of SR (Figure 7b, Table 4). The burned treatment spring 2012 ($F_{(1,11)}$=5.17, p=0.09, R^2=24) sampling period regression analysis indicated a positive trend between soil temperature and SR (Figure 7a, Table 4).

Table 3

T test for Efflux vs Soil Temperature by Treatment across Season

Season	Measurement	t-ratio	df	*p*-value
Spring 2012	LW	3.64	30	0.0014*
	SR	0.72	29	0.48
	ST	0.18	29	0.86

T-test analyses by treatment for litter weight (LW), soil CO_2 efflux (SR, µmol m-2 sec-1), and soil temperature (ST, °C)

Linear regressions were used to determine the relationships among SR to soil temperature (Figure 6, Table 4). Regressions between SR and soil temperature indicated positive relationship between soil temperature and SR, although the relationship was only statistically significant in the unburned plots (p=0.02, R^2=0.32) (Figure 6 B, Table 4). The burned plot showed a strong trend towards soil temperature having a positive relationship to SR (p=0.09, R^2=24) (Figure 6 A, Table 4).

Burned Unburned

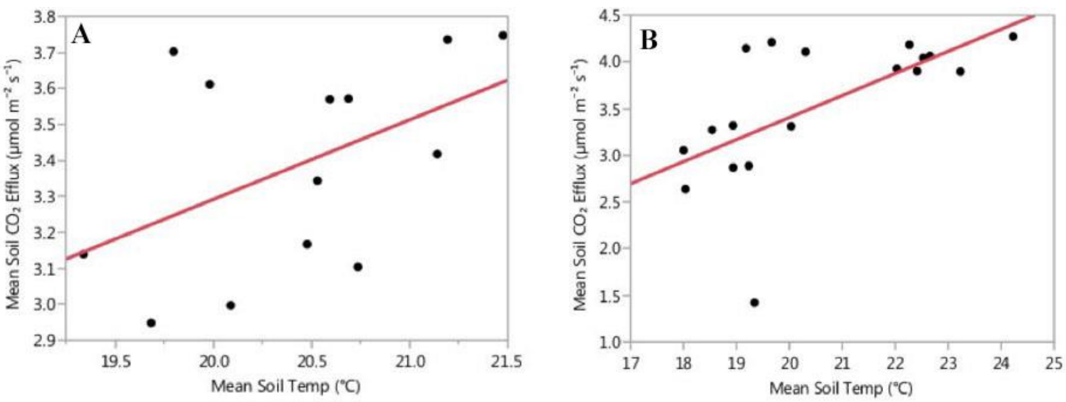


Figure 6. Linear Regression SR vs ST by Treatment for Spring 2012

A. Mean soil temperature (°C) vs. mean soil CO_2 efflux (µmol m^{-2} sec^{-1}) for the burned treatment (n=13) and B. mean soil temperature vs mean soil efflux (µmol m^{-2} sec^{-1}) for the unburned treatment (n=16), red lines show the linear fit against the plotted means.

Table 4

Linear Regression for Soil CO_2 Efflux vs Soil Temperature (Spring 2012)

Treatment	Variables	F-ratio	df	R^2	*p*-value
Burned	SR X ST	3.39	1,11	0.24	0.09
Unburned	SR X ST	6.52	1,14	0.32	0.02

Results of regression analyses for soil temperature (ST) as a predictor of soil CO_2 efflux (SR) by treatment, the first value under degrees of freedom (df) represents the model's df, the second value represents the error df.

Post-burn I Summer 2012 Sampling Period

Burned plots had significantly lower SR during the sampling period immediately following the prescribed fire (p<0.0001) (Table 5). SR in unburned plots (n=59, mean=4.28 µmol m^{-2} sec^{-1}, ± SE=0.09) was 42.3% greater than the burned plots (n=44, mean=3.0 µmol m^{-2} sec^{-1}, ± SE=0.07) (p<0.0001) (Figure 7, Table 5).

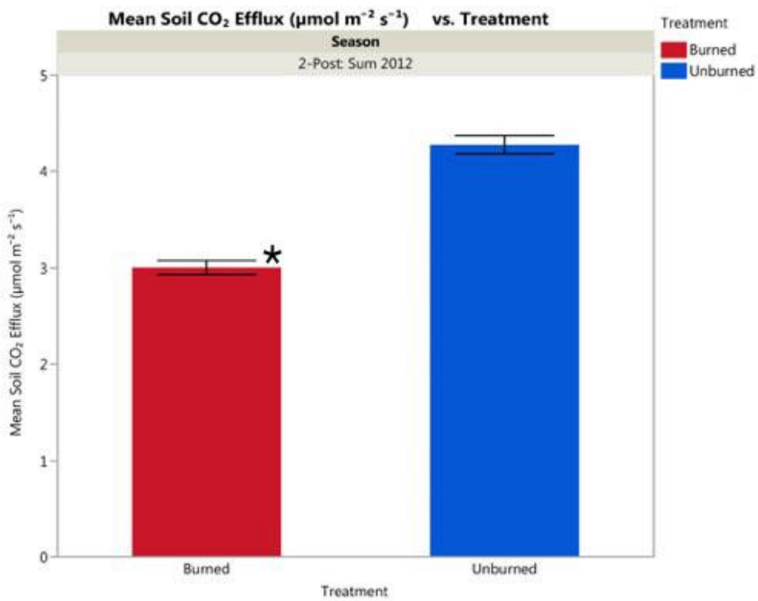


Figure 7. Mean SR by Treatment for Summer 2012

Mean soil CO_2 efflux (μmol m^{-2} sec^{-1}) from post-burn I sampling period (Summer 2012) with ± SE (Burned: n=44, Unburned: n=59).

The mean soil temperature was 2.2°C higher in burned plots than in unburned plots during the summer 2012 sampling period. This difference was significant (n=44, mean=26.72°C, and ± SE=0.31, burned; n=59, mean=24.49°C, and ± SE=0.15, unburned) ($p<0.0001$) (Figure 8, Table 5).

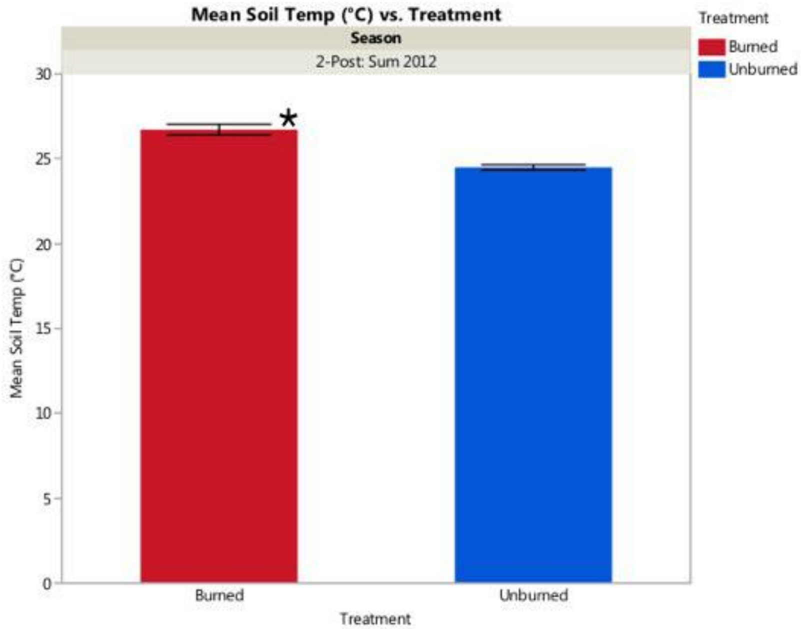


Figure 8. Mean ST by Treatment for Summer 2012

Mean soil temperature (°C) from post-burn I sampling period (Summer 2012) with ± SE (Burned: n=44, Unburned: n=59).

Table 5

T test for Efflux vs Soil Temperature (Summer 2012)

Season	Measurement	t-ratio	df	*p*-value
Summer 2012	SR	10.67	101	0.0001*
	ST	-6.39	101	0.0001*

T-test analyses by treatment for soil CO_2 efflux (SR, µmol m^{-2} sec^{-1}) and soil temperature (ST, °C).

Relationships between measured SR and soil temperature in the post-burn summer 2012 sampling period were examined using linear regressions (Figure 9, Table 6). Only the burned plots showed a significant effect of soil temperature on SR (p=0.02) although only 12% of the variability in SR was explained by soil temperature (Figure 9, Table 6).

Burned Unburned

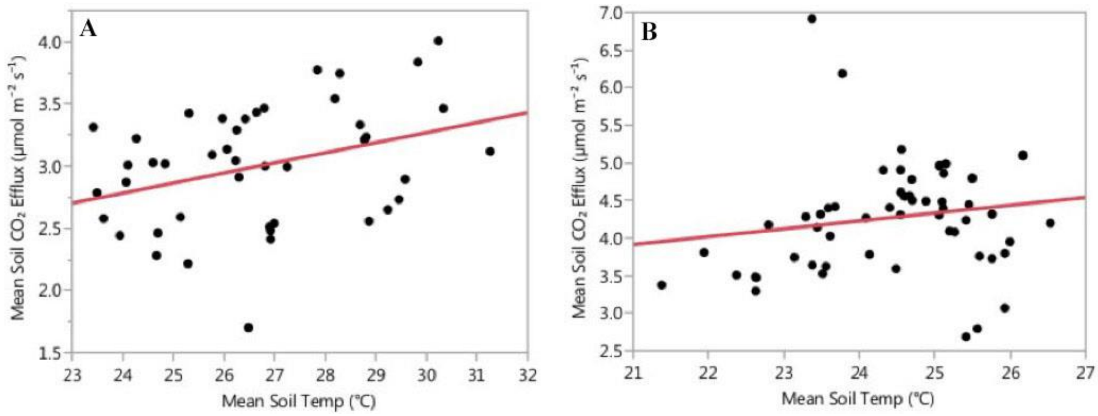


Figure 9. Linear Regressions SR vs ST for Summer 2012

A. Mean soil CO_2 efflux (µmol m^{-2} sec^{-1}) vs. mean soil temperature (°C) for the burned treatment (n=44), B. mean soil CO_2 efflux vs. mean soil temperature for the unburned treatment (n=61), red lines show the linear fit against the plotted means.

Table 6

Linear Regressions for Soil CO_2 Efflux vs Soil Temperature (Summer 2012)

Treatment	Variables	F-ratio	df	R^2	*p*-value
Burned	SR X ST	5.79	1,42	0.12	0.02*
Unburned	SR X ST	1.79	1,59	0.03	0.18

Results of regression analyses for soil temperature (ST) as a predictor of soil CO_2 efflux (SR) by treatment, the first value under degrees of freedom (df) represents the model's df, the second value represents the error df.

Post-burn II Fall 2012 Sampling Period

Six months after the prescribed fire, mean SR measurements continued to be significantly greater (p=0.013) in unburned plots (n=11, mean=2.18 µmol m^{-2} sec^{-1}, and ± SE =0.19) than the burned plots (n=11, mean=1.57 µmol m^{-2} sec^{-1}, and ± SE =0.11) (Figure 10, Table 7). Mean soil temperature was not significantly different between burned and unburned plots (burned, n=11, mean=13.65 °C, and ± SE =0.92; unburned, n=11, mean=14.17 °C, and ± SE =0.54; *p*=0.63) (Figure 11, Table 7).

Linear regressions showed that SR and soil temperature on the burned treatment continued to be significantly positively related in the fall following the prescribed fire (*p*=0.0015) (Figure 12 A, Table 8). SR and soil temperature were also positively related in the unburned plots although this effect was strongly trending toward significance (*p*=0.06) (Figure 12 B, Table 8).

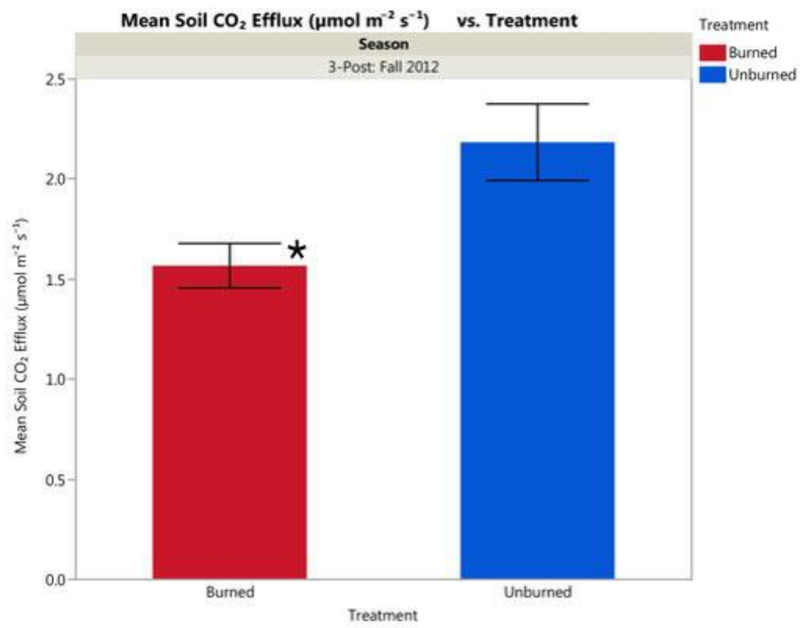


Figure 10. Mean ST by Treatment for Fall 2012

Mean soil CO_2 efflux (μmol m^{-2} sec^{-1}) from post-burn II sampling period (Fall 2012) with ± SE (Burned: n=11, Unburned: n=11).

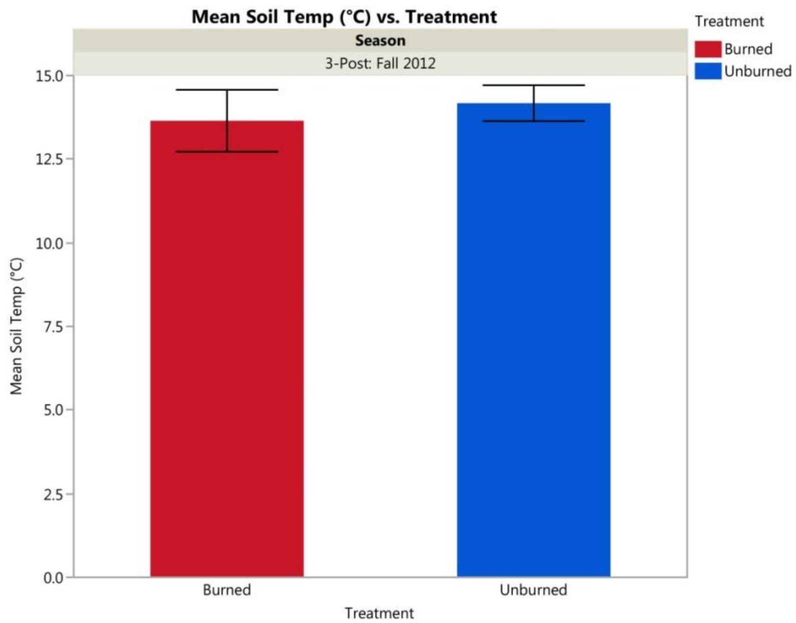


Figure 11. Mean ST by Treatment for Fall 2012

Mean soil temperature (°C) from post-burn II sampling period (Fall 2012).with ± SE (Burned: n=11, Unburned: n=11).

Table 7

T test for Efflux vs Soil Temperature (Fall 2012)

Season	Measurement	t-ratio	df	*p*-value
Fall 2012	SR	2.79	20	0.013*
	ST	0.49	20	0.63

T-test analyses by treatment for soil CO_2 efflux (SR, µmol m-2 sec-1) and soil temperature (ST, °C).

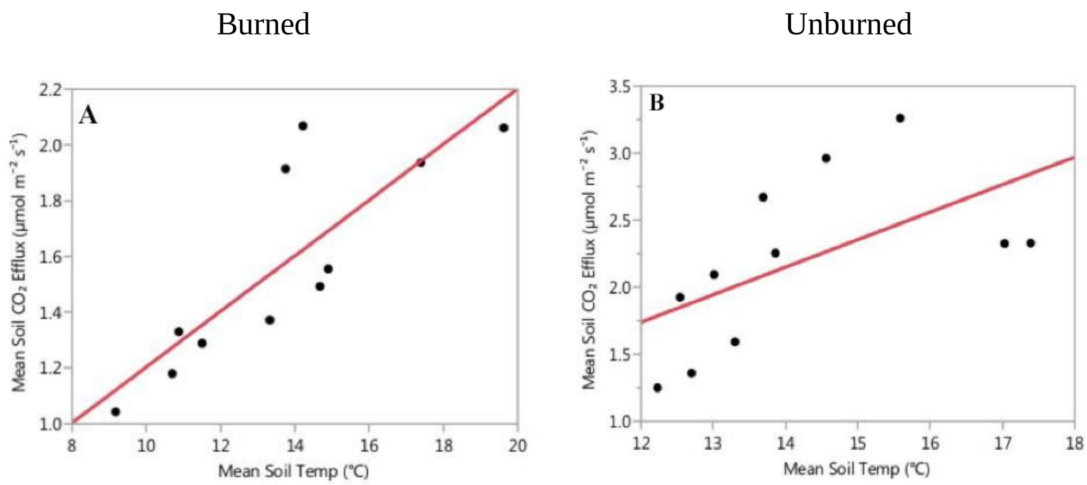


Figure 12. Linear Regressions SR vs ST by Treatment for Fall 2012

A. Mean soil CO_2 efflux (µmol m^{-2} sec^{-1}) vs. mean soil temperature (°C) for the burned treatment (n=11), B. mean soil CO_2 efflux vs. mean soil temperature for the unburned treatment (n=11), red lines show the normal linear fit against the plotted means.

Table 8

Linear Regressions for Soil CO_2 Efflux vs Soil Temperature (Fall 2012)

Treatment	Variables	F-ratio	df	R^2	*p*-value
Burned	SR X ST	20.15	1,9	0.69	0.0015*
Unburned	SR X ST	4.47	1,9	0.33	0.06

Results of regression analyses for soil temperature (ST) as a predictor of soil CO_2 efflux (SR) by treatment, the first value under degrees of freedom (df) represents the model's df, the second value represents the error df.

Post-burn III Spring 2013 Sampling Period

Nine months after the prescribed fire, mean SR measurements continued to be significantly greater for the unburned plots (n=14, mean=1.73 µmol m^{-2} sec^{-1}, and ± SE =0.09) than the burned plots (n=14, mean=1.25 µmol m^{-2} sec^{-1}, and ± SE=0.07) (p<0.0002) (Figure 13, Table 9). Mean soil temperature readings for the burned (n=14, mean=13.99 °C, and ± SE=0.43) and unburned (n=14, mean=14.27 °C, and ± SE =0.28) remained not statistically different (*p*=0.58) (Figure 14, Table 9).

Linear regressions showed that the relationship between mean SR and soil temperature in burned plots were not significant (*p*=0.54) for the spring 2013 sampling period (Figure 15a, Table 10). Mean SR and soil temperature, however, were significantly related (*p*=0.03) in the unburned plots (Figure 15b, Table 10). While the effect was statistically significant, soil temperature only explained 33% of the variability seen in SR (Figure 15b).

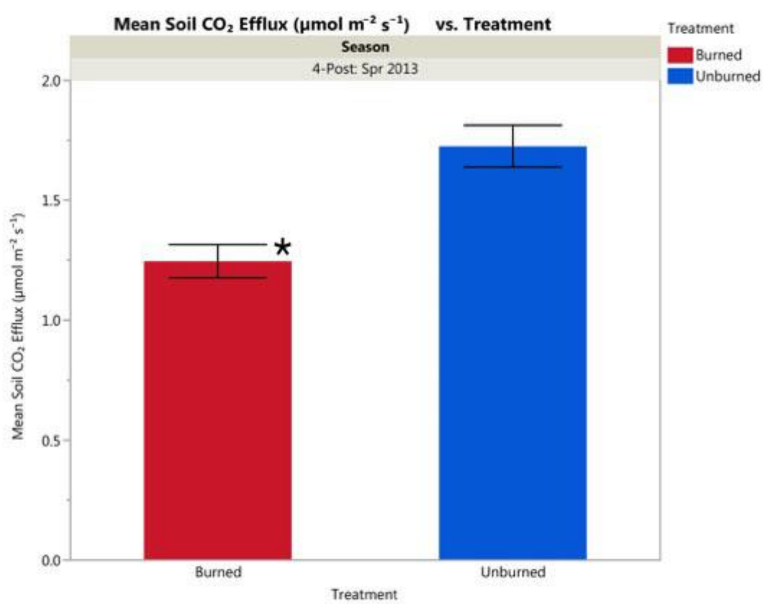


Figure 13. Mean SR by Treatment for Spring 2013

Mean soil CO_2 efflux (μmol m^{-2} sec^{-1}) from post-burn III sampling period (Spring 2013) with ± SE (Burned: n=14, Unburned: n=14).

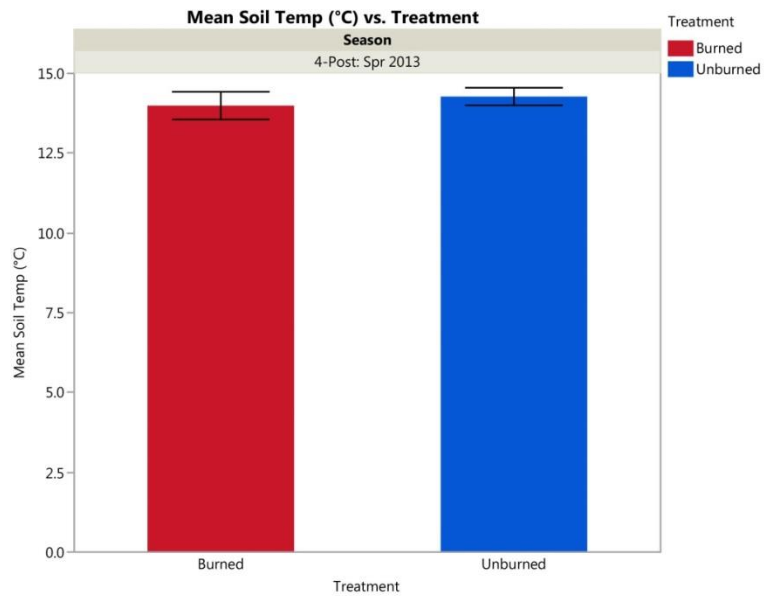


Figure 14. Mean ST by Treatment for Spring 2013

Mean soil temperature (°C) from post-burn III sampling period (Spring 2013).with ± SE (Burned: n=14, Unburned: n=14).

Table 9

T test for Efflux vs Soil Temperature by Treatment across Season

Season	Measurement	t-ratio	df	*p*-value
Spring 2013	SR	4.29	26	0.0002*
	ST	0.56	26	0.58

Compiled t test analyses for soil efflux (SR) and soil temperature (ST).

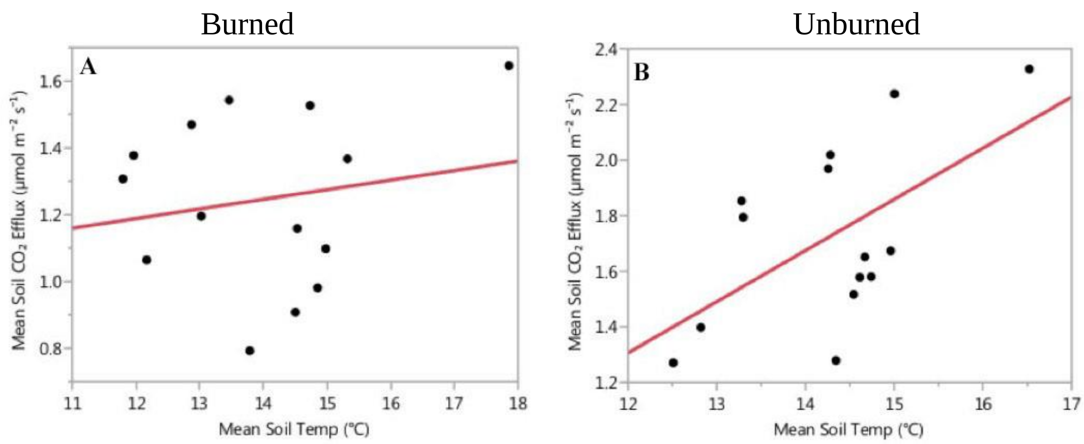


Figure 15. Linear Regressions SR vs ST by Treatment for Spring 2013

A. Mean soil CO_2 efflux (µmol m^{-2} sec^{-1}) vs. mean soil temperature (°C) for the burned treatment (n=14) and B. mean soil CO_2 efflux vs. mean soil temperature for the unburned treatment (n=14), red lines show the linear fit against the plotted means.

Table 10

Linear Regressions for Soil CO_2 Efflux vs Soil Temperature (Spring 2013)

Treatment	Variables	F-ratio	df	R^2	*p*-value
Burned	SR X ST	0.41	1,12	0.03	0.54
Unburned	SR X ST	6.02	1,12	0.33	0.03*

Results of regression analyses for soil temperature (ST) as a predictor of soil CO_2 efflux (SR) by treatment, the first value under degrees of freedom (df) represents the model's df, the second value represents the error df.

Overall Analyses

Over the course of the study, 16,630 SR measurements (µmol m^{-2} sec^{-1}) were collected. There were 9,087 SR measurements collected in the burned plots (min=0.5, max=7.05) and 7,053 measurements from the unburned plots (min=0.51, max=9.31). Measurements collected on a given day were averaged to obtain daily mean SR values within treatment resulting in a total sample size of 184 daily means (Table 11). Overall mean SR across treatments was 3.13 µmol m^{-2} sec^{-1} (± SE=0.09). When all daily means for all collection periods were compared, SR for unburned plots (n=102, mean=3.57µmol m^{-2} sec^{-1}, and ± SE=0.12) was 38.9% greater than SR in burned plots (n=82, mean=2.57 µmol m^{-2} sec^{-1}, and ± SE=0.1) (Figure 16).

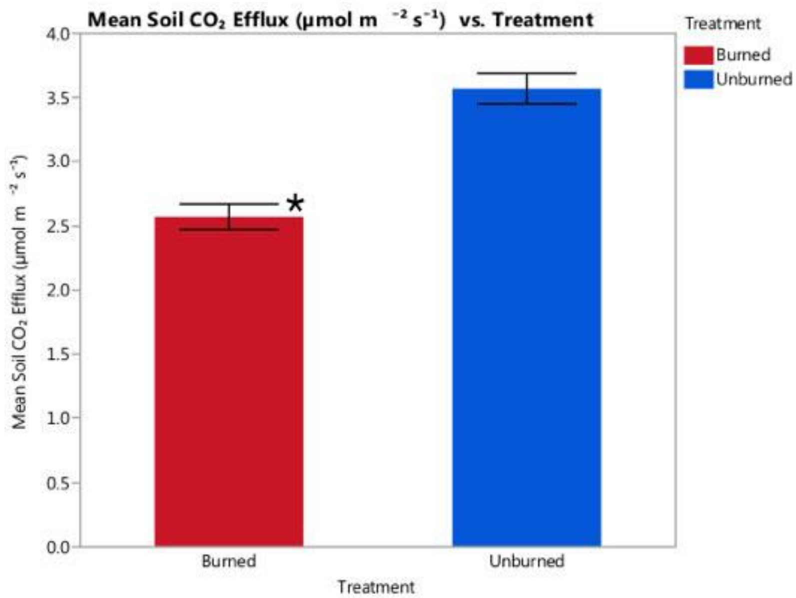


Figure 16. Mean SR by Treatment for Combined Sampling Periods

Overall mean soil CO_2 efflux rates (µmol m^{-2} sec^{-1}) for all sampling dates (2012-2013) with ± SE (Burned: n=82, Unburned: n=102).

Table 11

Sample Size, Mean, & SE for SR & ST by Treatment & Season

Season	Measurement	Treatment	Mean	SE	Sample Size
Spring 2012	SR	B	3.39	0.08	13
		UB	3.53	0.18	18
	ST	B	20.44	0.18	13
		UB	20.53	0.46	18

Table 11 (continued).

Summer 2012	SR	B	3.0	0.07	44
		UB	4.28	0.09	59
	ST	B	26.72	0.31	44
		UB	24.49	0.15	59
Fall 2012	SR	B	1.57	0.11	11
		UB	2.18	0.19	11
	ST	B	13.65	0.92	11
		UB	14.17	0.54	11
Spring 2013	SR	B	1.25	0.07	14
		UB	1.73	0.09	14
	ST	B	13.99	0.43	14
		UB	14.28	0.28	14

Sample size, mean, and standard error (SE) for soil CO_2 efflux (SR) and soil temperature (ST) by treatment across season 2012 & 2013.

A nested, mixed block ANOVA was used to test SR data between treatments and across season for significance (Figure 17, Table11). Treatment (i.e., fire) and season were both fixed factors with treatment having two levels (burned and unburned) and season having four levels (pre-burn, post-burn I, post-burn II, and post-burn III). Plot was included in the analysis as a block, nested within burn treatment (burned = plots 5-8, and unburned = plots 9-12), to account for any variability among the treatment plots.

The ANOVA results showed significant effects of both treatment and season on mean SR, but a significant treatment x season interaction ($F_{(3,170)}$ =9.6, p<0.0001) precluded direct interpretation of these hypothesis tests. To further examine this interaction, a Tukey's post hoc (HSD) test was used to determine the differences between the treatments across the seasons. Mean SR rates did not significantly differ between the burned and unburned treatments in the pre-burn sampling period. However, immediately following the burn, the mean SR rates were significantly higher in the unburned plots. The unburned treatment retained higher mean SR through the two subsequent sampling intervals, but the overall SR levels declined and the difference between these two treatments lessened over these two seasons (Figure 17).

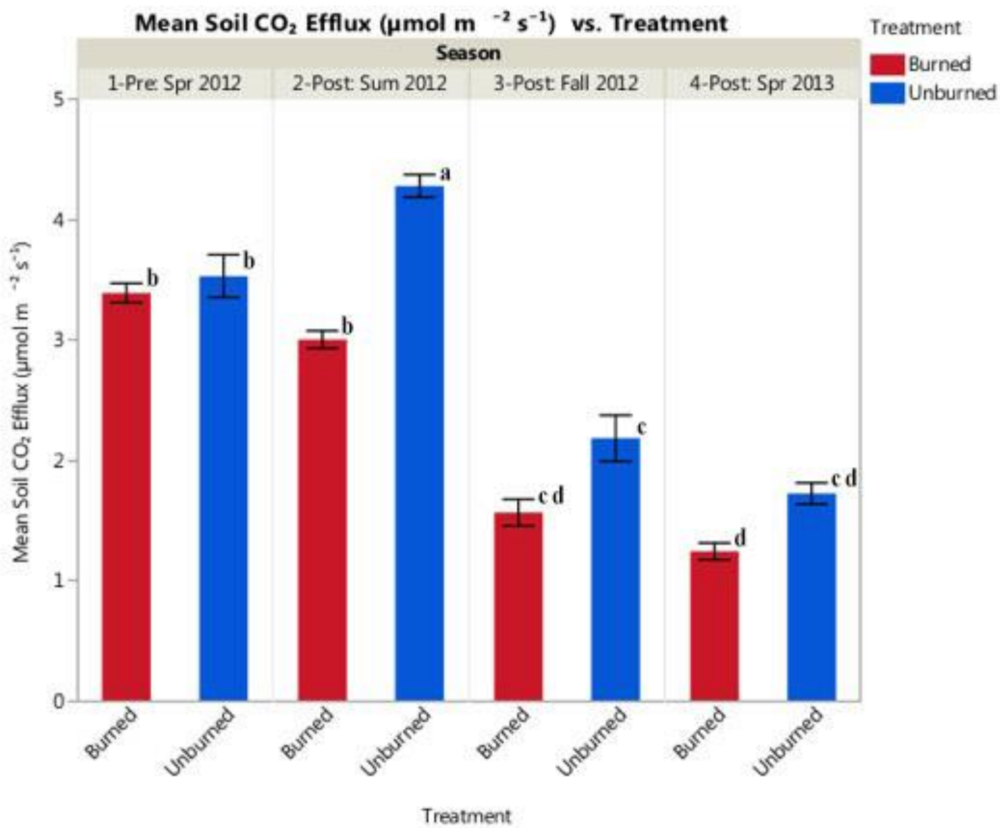


Figure 17. Mean SR by Treatment across Season

Mean soil CO_2 efflux rates (μmol m^{-2} sec^{-1}) for treatment and season all sampling dates (2012-2013) with ± SE (n=184).

Table 12

Nested, Mixed Model ANOVA Analysis for Soil CO_2 Efflux

Factor	df	F ratio	*p*-value
Treatment	1,170	6.23	0.043
Season	3,170	142.74	< 0.0001
Treatment X Season	3,170	9.63	< 0.0001*
Plot [Treatment]	6,170	4.22	<0.0006

There were a total of 14,461 soil temperature measurements collected over all four sampling dates. There were 9,276 soil temperature measurements collected in the burned plots (min=7.5°C, max=35.4°C) and 5,185 measurements from the unburned plots (min=10.4°C, max=29.2°C). Measurements collected on a given day were averaged to obtain daily mean soil temperature values within treatment resulting in a total sample size of 184 daily means. Overall mean soil temperature across treatments was 21.5°C (± SE=0.39). When all daily means for all collection periods were compared, mean soil temperature for the burned plots (n=82, mean=21.79°C, and ± SE=0.67) were not statistically different (*p*=0.73) from the mean soil temperature on unburned plots (n=82, mean=21.28°C, and ± SE=0.45) (Figure 18).

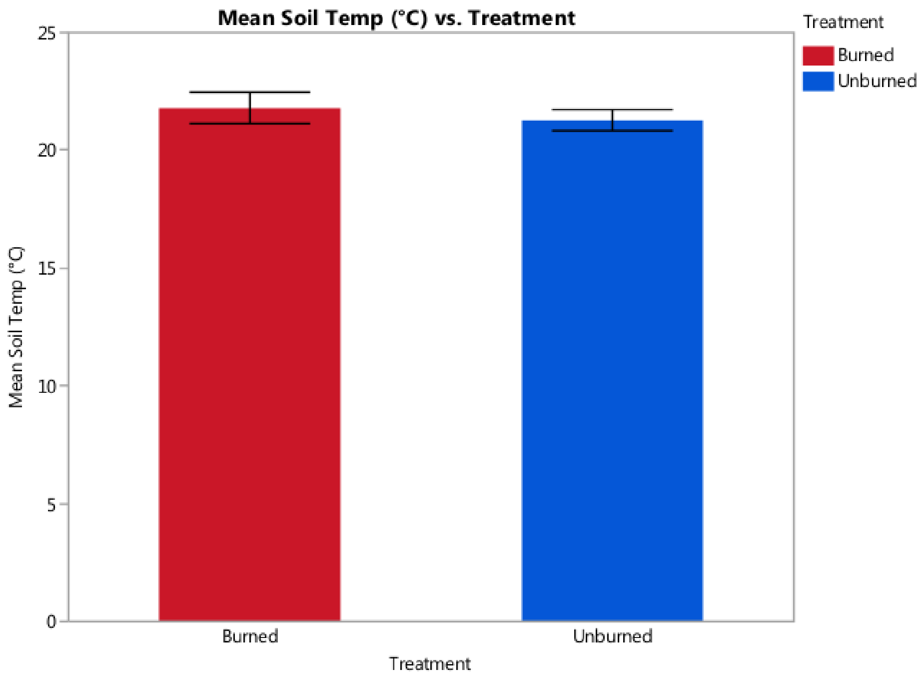


Figure 18. Mean ST for Combined Sampling Periods

Overall mean soil temperature (°C) for all sampling dates (2012-2013) with ± SE (Burned: n=82, Unburned: n=102).

A nested, mixed block ANOVA was used to test soil temperature (°C) data between treatments and across season for significance (Figure 17, Table11). Treatment (i.e., fire) and season were both fixed factors with treatment having two levels (burned and unburned) and season having four levels (pre-burn, post-burn I, post-burn II, and post-burn III). Plot was included in the analysis as a block, nested within burn treatment (burned = plots 5-8, and unburned = plots 9-12), to account for any variability among the treatment plots.

The ANOVA results showed significant effects of both treatment and season on mean soil temperature, but a significant treatment x season interaction ($F_{(3,170)}$ =8.8, p<0.0001) precluded direct interpretation of these hypothesis tests (Table 13). To further examine this interaction, a Tukey's post hoc (HSD) test was used to determine the differences between the treatments across the seasons. The mean burned treatment soil temperature readings in the sampling period after the prescribed burn were statistically the highest across this experiment, followed by the unburned treatment post-burn soil temperature measurements. The pre-burn mean soil temperature measurements on both treatments were not statistically different, although were statistically lower than the post-burn measurements from both groups. Both treatments mean soil temperature readings were the lowest for the following sampling periods (Figure 19).

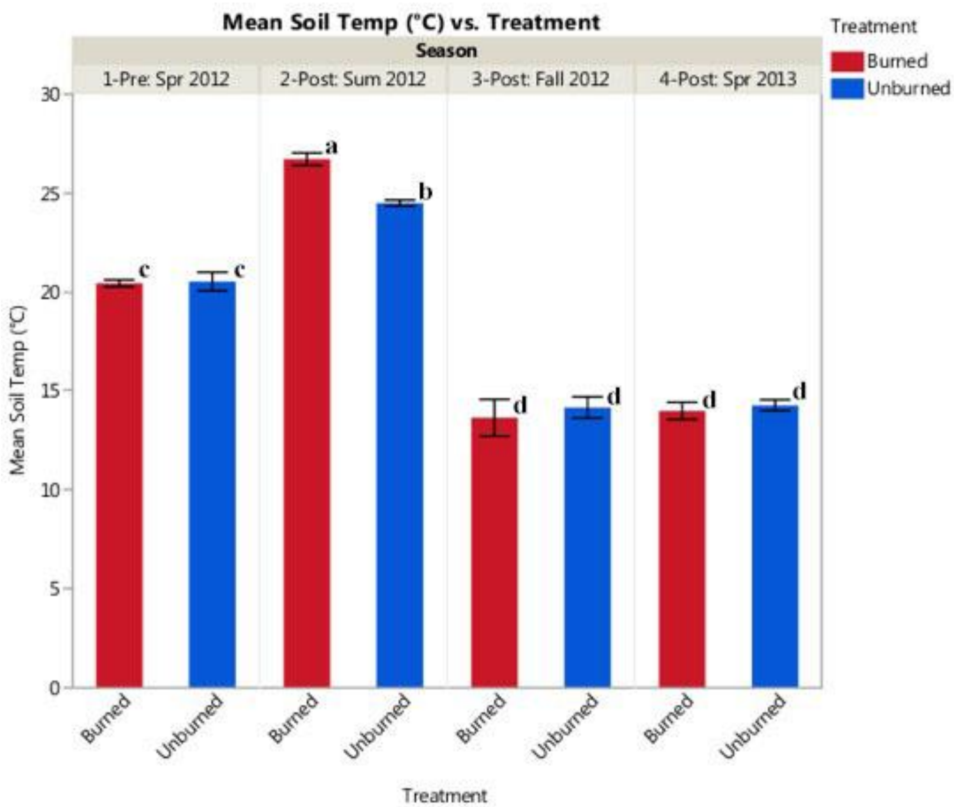


Figure 19. Mean ST by Treatment across Season

Mean soil temperature (°C) by burn treatment across season (2012 and 2013). The burned treatments are red and the unburned treatments are blue, ± standard error bars are displayed above each treatment group (n=184).

Table 13

Nested, Mixed Model ANOVA Analysis for Soil Temperature

Factor	df	F ratio	*p*-value
Treatment	1,170	0.13	0.73
Season	3,170	570.03	< 0.0001
Treatment X Season	3,170	8.8	< 0.0001*
Plot [Treatment]	6,170	7.7	<0.0006

A linear regression was used to predict SR (µmol m^{-2} sec^{-1}) in relation to soil temperature (°C) using overall daily mean SR and daily mean soil temperature measurements (Appendix B). This regression pooled SR and soil temperature measurements from both treatments across season for this analysis and showed a strong positive correlation between soil temperature and soil CO_2 efflux ($F_{(1,182)}$=157.59, p <0.0001; R^2=0.46) (Figure 21).

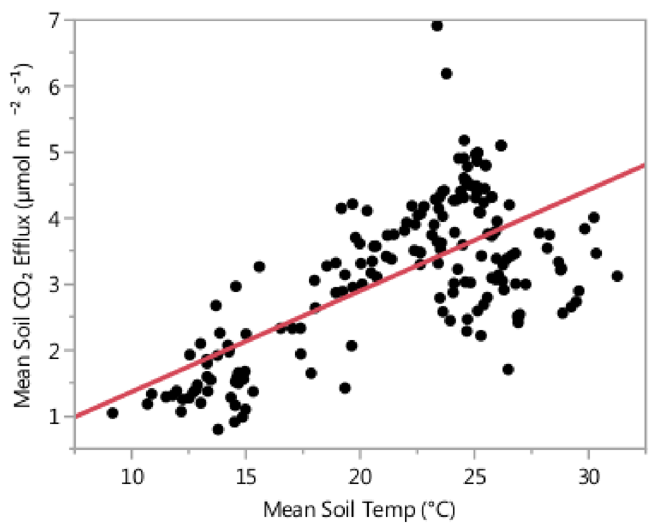


Figure 20. Linear Regression SR vs ST for Combined Sampling Periods

Regression for mean soil CO_2 efflux (μmol m^{-2} sec^{-1}) by mean soil temperature (°C) for the all burned and unburned data (n=184), red line shows the linear fit against the plotted means.

Two additional linear regressions were used to predict SR (μmol m^{-2} sec^{-1}) in relation to soil temperature (°C) within treatment groups. These regressions showed strong positive effects for both the burned treatment ($F_{(1,80)}$=114.3, p <0.0001; R^2=0.59) and the unburned treatment ($F_{(1,100)}$=239.88, p <0.0001; R^2=0.71) across all sampling dates (Figure 21 A & B). Although strong relationships were shown in both treatments, soil temperature explained more variability in SR from the unburned treatment (71%) than that of the unburned treatment (59%).

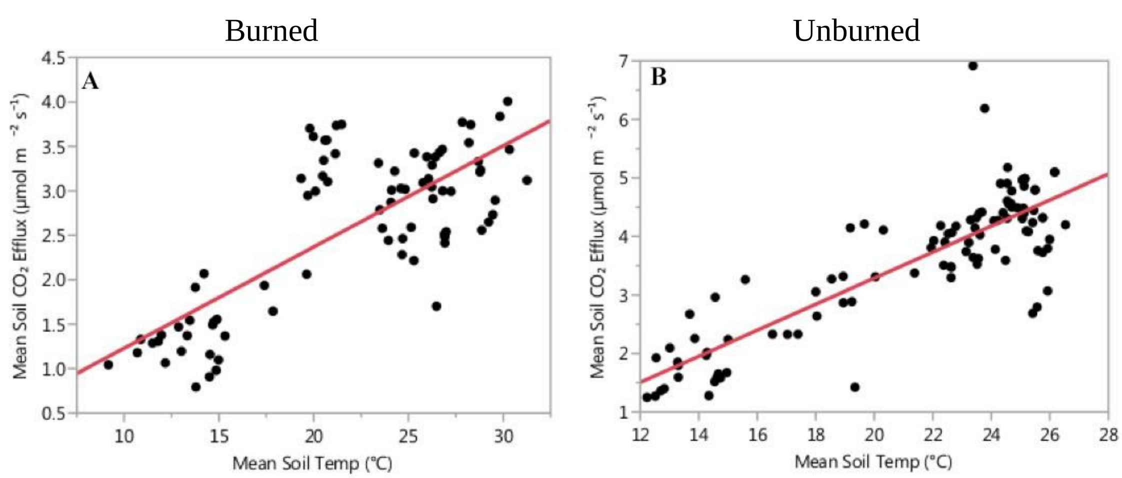


Figure 21. Linear Regressions SR vs ST by Treatment for Combined Sampling Periods

A. Mean soil CO_2 efflux (μmol m^{-2} sec^{-1}) vs. mean soil temperature (°C) for the burned (n=82) and B. mean soil CO_2 efflux vs. mean soil temperature for the unburned data (n=102), red line shows the linear fit against the plotted means.

CHAPTER IV – DISCUSSION

Fire had a dramatic effect on soil respiration in this study. For at least nine months following a prescribed fire, SR rates were significantly lower in burned longleaf pine stands compared to those in unburned longleaf pine stands (overall means: 2.57 µmol m^{-2} sec^{-1} versus 3.57 µmol m^{-2} sec^{-1} , respectively; Figure 16). The greatest difference in soil CO_2 efflux rates between burned and unburned sites occurred during the months immediately after the prescribed fire.

Effects of fire on SR are variable and often depend on moisture. A study from an African savannah showed that SR was decreased after a fire but after a rain event was two times higher than unburned areas. This short-term pulse in SR was believed to be due to an increase in labile C and nutrients in the dissolved ash (Andersson et al., 2004). Fultz et al., (2016) observed a sharp increase in SR in one site immediately post-fire (0.5 h) but otherwise noted no differences in SR among burned sites and unburned reference areas. We did not measure soil moisture in our study; however, litter consumption in the burned plots likely influenced the soil moisture retention capacity of these soils. If so, then reduced soil moisture may help explain the reduced SR rates in burned plots.

Nutrient availability also influences SR and fire can significantly alter nutrient flow in forest ecosystems. Nitrogen can be removed by a fire by volatilization, although the ash from fuels consumed by fire can increase soil levels of NH_4 and NO_3 (Covington & Sackett 1986, Weston & Attiwill 1990, Certini 2005). Fire intensity also regulates nutrient loss following a fire. Needle fall and ash can play important roles in decreasing surface runoff post-burn before re-emergence of vegetation (Cerda & Doerr 2008). In addition, high intensity fires can release hydrophobic residues from ash that can transfer into the upper mineral layers of the soil, increasing the potential for more runoff over time with more frequent high intensity fires (Debano 2000). Although soil carbon and nutrients were not measured in this study, they could have given more insight into the autotrophic/heterotrophic response mechanisms to the prescribed burn.

Litter mass has been shown to be positively correlated with SR rates in other forest ecosystems (Sulzman et al. 2005, Metcalfe et al. 2007); however, pre-burn SR was not affected by litter mass in our study. Although litter weights (g) collected during the pre-burn spring 2012 sampling period were significantly higher (Figure 3) on the unburned treatment as compared to the burned treatment, SR did not differ between burned and unburned treatments.

Fire intensity may also influence SR rates; Wüthrich et al. (2002) observed increased SR rates following a fire with double fuel loads. These rates remained higher than unburned reference sites for up to five months post fire and returned to normal a year later. In a study by Buckingham et al. (2015) in Australia, a site that experienced differing fire severities showed that litter decomposition rates can normalize after a 3 year absence of fire. Our study showed sharp decrease in SR in the burned areas. Nevertheless, our data show a recovery similar to the one observed in the study by Wüthrich et al. (2002). Although CO_2 efflux rates were still lower in burned areas nine months post-fire, the magnitude of the difference between burned and unburned sites was smaller indicating that soil respiration in burned areas was recovering. This post-fire recovery is consistent with our pre-burn SR data. The pre-burn SR readings in the burned and unburned plots were not significantly different from each other (Figure 4). The plots in the burned treatments had been burned previously in 2010; thus if any post-fire effects on SR were present, they had disappeared within two years.

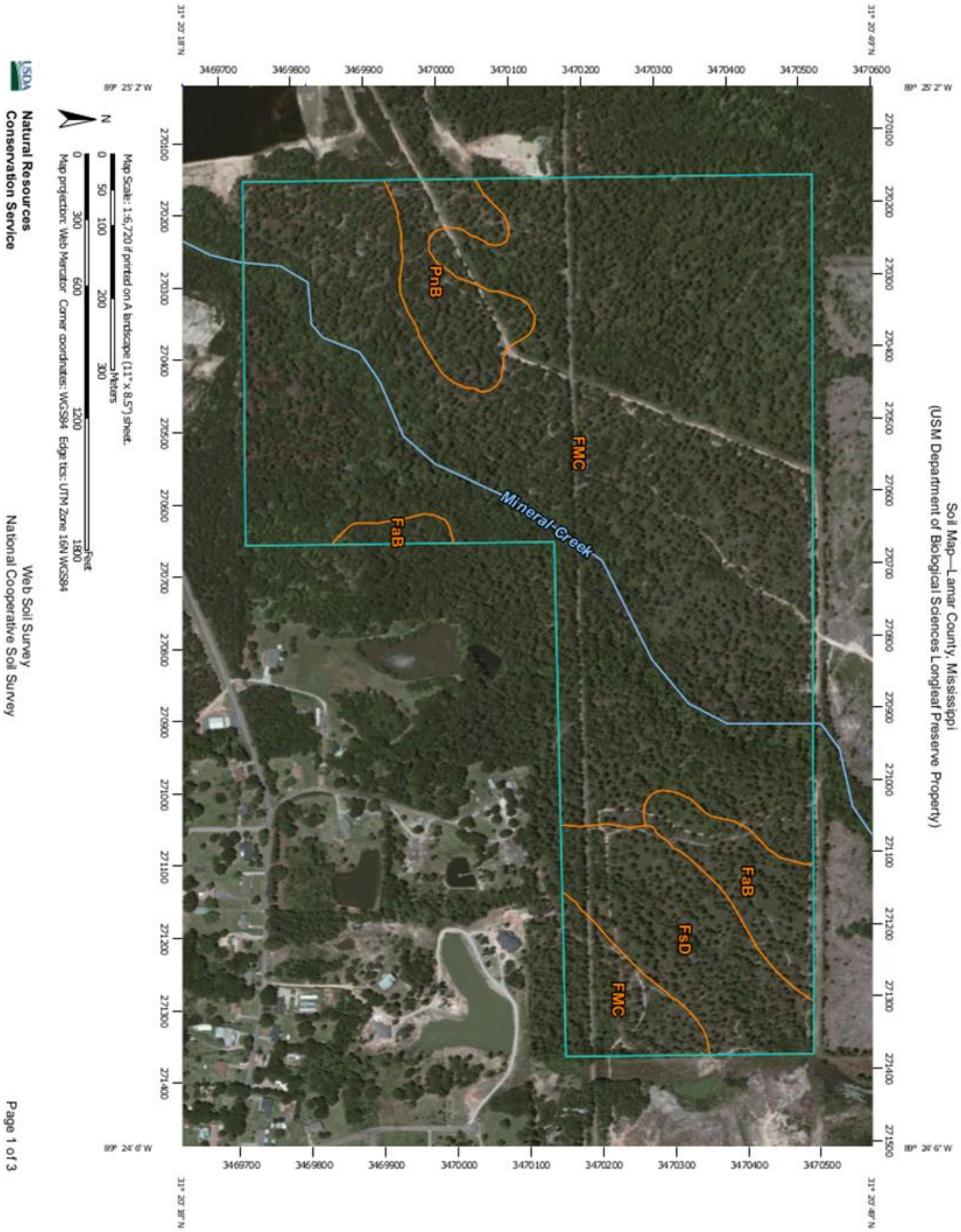
Soil temperature and SR are often positively linked and this was the case in our study (Fang & Moncrieff 2001, Almagro et al. 2009). Regressions showed that soil temperature explained 59% of the variability in SR on the burned treatment and 71% of the variability in SR on the unburned treatment across all seasons (Figure 21). These results indicate that the unburned treatment had stronger positive relationship between soil temperature and SR than the burned treatment. This effect may be explained by decreased soil moisture in burned plots due increased soil exposure to solar radiation.

While this study primarily focused on bulk SR pre- and post-burn, the variable (microbial/root/invertebrate) sources of the SR rates observed on the experimental treatments were not identified. Further research is needed to elucidate the factors leading to SR rates following a prescribed burn, specifically the changes in plant, microbial & invertebrate community structures following a prescribed burn. Quantifying the sources of respiration (heterotrophic/autotrophic) following a fire is essential to understanding the community response (Certini 2005). Further sampling of the organic horizon and the litter contributions on burned and unburned treatments would shed more light on the exact origins, likely microbial (bacterial/fungal) of the SR increases. Quantifying the effects fire has on plant roots (autotrophic) is essential to determine the contribution from the vegetation to overall SR rates across the treatment groups on the LLP. In order to better access plant root activity, ingrowth cores established across the treatment plots would elucidate the effects of the prescribed burn on root mortality and regeneration.

While there have been numerous studies estimating SR rates from forest understories with eddy covariance techniques (open-path IRGA) (Tang et al. 2006, Vargas et al. 2010, Whelan et al. 2013), until recently fewer studies on SR rates from forest understories have been conducted with closed chamber IRGA systems due to inherent difficulties in collecting these measurements (Xie et al. 2009, Ruehr & Buchmann 2009, Wang et al. 2010). Closed path IRGA systems encounter obstacles that have to be overcome such as chamber heating and altered gas diffusion rates (Welles et al. 2001). The IRGA (LICOR LI-8100) used in this experiment allows the user to collect fine-scale respiration data over long periods of time.

Understanding the carbon and nutrient dynamics within the upper layers of soil and understory in terrestrial forest ecosystems in relation to fire is necessary to fully understand the effects of these fires. The southeastern United States is composed of many ecosystems that are maintained by fire. In the absence of fire, leaf litter and woody debris accumulation provides fuel loading that can lead to devastating fires causing excessive tree mortality and ecosystem damage (Varner et al. 2005) as well as increased wildfire gas emissions (Sommers 2014). This research has practical applications for advancing our understanding of ecosystem responses, specifically SR, from prescribed burning in longleaf pine savannas and forests in relation to general ecosystem functioning and services. Future studies should examine post-fire nutrient dynamics and soil microbial activity to further elucidate the effects of fire on soil respiration

APPENDIX A – NRCS Soil Survey



MAP LEGEND

Area of Interest (AOI)
- Area of Interest (AOI)

Soils
- Soil Map Unit Polygons
- Soil Map Unit Lines
- Soil Map Unit Points

Special Point Features
- Blowout
- Borrow Pit
- Clay Spot
- Closed Depression
- Gravel Pit
- Gravelly Spot
- Landfill
- Lava Flow
- Marsh or swamp
- Mine or Quarry
- Miscellaneous Water
- Perennial Water
- Rock Outcrop
- Saline Spot
- Sandy Spot
- Severely Eroded Spot
- Sinkhole
- Slide or Slip
- Sodic Spot
- Spoil Area
- Stony Spot
- Very Stony Spot
- Wet Spot
- Other
- Special Line Features

Water Features
- Streams and Canals

Transportation
- Rails
- Interstate Highways
- US Routes
- Major Roads

Background
- Aerial Photography

MAP INFORMATION

The soil surveys that comprise your AOI were mapped at 1:20,000.

Warning: Soil Map may not be valid at this scale.

Enlargement of maps beyond the scale of mapping can cause misunderstanding of the detail of mapping and accuracy of soil line placement. The maps do not show the small areas of contrasting soils that could have been shown at a more detailed scale.

Please rely on the bar scale on each map sheet for map measurements.

Source of Map: Natural Resources Conservation Service
Web Soil Survey URL: http://websoilsurvey.nrcs.usda.gov
Coordinate System: Web Mercator (EPSG:3857)

Maps from the Web Soil Survey are based on the Web Mercator projection, which preserves direction and shape but distorts distance and area. A projection that preserves area, such as the Albers equal-area conic projection, should be used if more accurate calculations of distance or area are required.

This product is generated from the USDA-NRCS certified data as of the version date(s) listed below.

Soil Survey Area: Lamar County, Mississippi
Survey Area Data: Version 7, Dec 24, 2013

Soil map units are labeled (as space allows) for map scales 1:50,000 or larger.

Date(s) aerial images were photographed: Jan 22, 2010—May 6, 2010

The orthophoto or other base map on which the soil lines were compiled and digitized probably differs from the background imagery displayed on these maps. As a result, some minor shifting of map unit boundaries may be evident.

Map Unit Legend

Lamar County, Mississippi (MS073)			
Map Unit Symbol	**Map Unit Name**	**Acres in AOI**	**Percent of AOI**
FaB	Falkner silt loam, 2 to 5 percent slopes	8.0	5.0%
FMC	Freestone-McLaurin-Susquehanna association, rolling (freest-mclaurin-susquehanna)	129.2	81.0%
FsD	Freestone, Susquehanna, and Prentiss soils, 5 to 12 percent slopes (freest, susquehanna and prentiss)	14.2	8.9%
PnB	Prentiss fine sandy loam, 2 to 5 percent slopes	8.1	5.1%
Totals for Area of Interest		**159.5**	**100.0%**

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